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Demographic and Reproductive Traits of Blanding's Turtles, *Emydoidea blandingii*, at the Western Edge of the Species' Range

Sara Ruane¹, Stephen A. Dinkelacker², and John B. Iverson³

Conspecific turtle populations typically exhibit variation in demographic and reproductive traits such as adult size, growth rate, sex ratio, and clutch size. Variation in these traits has been previously correlated to variation in local environmental conditions, latitude, and habitats. Given that some turtle species have large geographic ranges and occur in a variety of habitats, it is imperative to determine how traits differ throughout the species' range. Towards this end, we examined demographic and reproductive traits of Blanding's Turtles (*Emydoidea blandingii*) in Grant County, Nebraska over the span of six years. The population's sex ratio was female biased (0.7:1.0, M:F) and skewed towards large, adult turtles (5:1, adult:juvenile). The analysis of adult survivorship suggests that female turtles (59% annual survivorship) may be experiencing greater mortality rates compared to males (90% annual survivorship), possibly due to road mortality. Unlike all previous reports, analyses of reproductive parameters indicate that turtles in the western Nebraska population do not increase clutch size with body size. Rather, egg size increases as body size increases, which may help reduce desiccation rates of the eggs in an arid environment. Optimal egg size may not be reached due to pelvic width constraints of females. Comparisons of our findings with those of other Blanding's Turtle studies are discussed.

TURTLE species are declining across the globe at alarming rates and are at high risk of extinction due to their life-history traits (Gibbons et al., 2000). Many turtles have a life-history strategy characterized by late maturity, high adult survivorship rates, low fecundity, and long life spans. Species with these traits may be particularly vulnerable to unnatural disturbances, such as introduced species, human exploitation, and habitat fragmentation (Klemens, 2000). Such characteristics make human-inflated rates of adult mortality in these species unsustainable (Congdon et al., 1993; Seigel and Dodd, 2000).

To best manage individual species of turtle, thorough examinations of turtle populations are crucial. For successful conservation, species found across broad geographic ranges require specific knowledge of how populations differ from each other in order to best assess conservation strategies (Crandall et al., 2000). It has been demonstrated that among populations of a particular turtle species, there is often variation in ecological aspects such as reproduction (Iverson and Smith, 1993; Iverson et al., 1997; Litzgus and Mousseau, 2006). For example, in some parts of their range, female Spotted Turtles (*Clemmys guttata*) may nest once per annum, whereas females in other populations of Spotted Turtles nest up to three times per annum (Litzgus and Mousseau, 2003). Variation in reproductive traits are found across multiple turtle species (including terrestrial, freshwater, and marine), and the variation may be due to differences in adult body size, age/size at maturity, latitude, or ultimately, resource accumulation (Iverson, 1992). Additionally, anthropogenic changes in the environment, such as the building of roadways, pollution, and global warming, also have the

ability to change demographic and reproductive traits for turtle populations (Janzen, 1994; Bishop et al., 1998; Aresco, 2005). With so much natural as well as artificially induced potential variation across populations of a single species, an understanding of the specific life history traits of individual populations is vital for efficient and appropriate management plans (Gibbons et al., 2000; Seigel and Dodd, 2000).

One turtle species known to show demographic and reproductive variation across its range (Ernst et al., 1994) is the Blanding's Turtle (*Emydoidea blandingii*), which occurs sporadically from western Nebraska to Nova Scotia and is centered around the Great Lakes region (Ernst et al., 1994). Blanding's Turtles are among the longest-lived freshwater turtles (>80 years; Congdon et al., 2001), and exhibit late maturity, high adult survivorship rates, and low annual fecundity (Congdon et al., 1993, 2000, 2001). Blanding's Turtles are locally endangered or threatened in many states and provinces, making detailed assessment of populations especially important for local management of this species. Differences in demography and reproductive ecology have been reported across the species' range (MacCulloch and Weller, 1988; Congdon and van Loben Sels, 1991; Joyal et al., 2000) and even within the same state (Rowe, 1992; Germano et al., 2000). In this study, we investigate a population of Blanding's Turtles originally studied by Rowe (1992) in western Nebraska over a period of six years. We report on population demography and reproductive traits, and compare our results to those from other populations. Because the population we examined was in anthropogenically altered habitat, our study also provides baseline data concerning how this species fares in disturbed situations.

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MATERIALS AND METHODS

Study sites.—Blanding's Turtles were studied near Hyannis, Grant County, Nebraska during the months of May and June from 2001–2004, late May through August in 2005, and late May through late July in 2006. Beem Lake (in Hyannis, 42°0'0"N, 101°45'39.6"W) and Doc Lake (13 km east of Hyannis, 42°2'13.1994"N, 101°32'34.8"W) are soft-bottomed lakes with abundant emergent and aquatic vegetation. Both have a two-track railway to the immediate north of the water. The tracks are physically impassable by Blanding's Turtles and so prevent turtles from traveling north of the lakes. Many female turtles have been observed nesting along the train tracks. A two-lane highway borders the southern edge of the lakes (see Rowe, 1992 for further description). The train tracks and highway are anywhere from approximately 2–200 m away from the waters' edge. Due to the presence of the railroad and the highway, the lakes are surrounded by substrates that would not be found under natural circumstances (rocks used as ballast for the train tracks abut directly with the lakes' shores on the north, while pavement and gravel border the lakes to the south). Additionally, Doc Lake has a small pond on the south side of the highway that was also surveyed and is considered part of the Doc Lake population. The data collected from Beem and Doc Lake were combined for all analyses in order to generalize about Blanding's Turtles at the extreme west of their range.

Turtle collection and demographic data.—We collected turtles by hand on land around the lake perimeters and from the water using fyke nets baited with rough-cut fish. Nets were placed mainly in areas near the shoreline with abundant emergent vegetation, where they were baited and checked daily. Nets were placed on the bottom of the lakes in water that was deep enough to fully submerge the throat of the net, yet shallow enough to allow captured animal to come to the surface to breath. We marked individual turtles using methods similar to Cagle (1939). We determined male turtles by the presence of concave plastrons, thickened tails, and darkened tomia (Ernst et al., 1994). Turtles lacking these characters and larger than the smallest gravid female found were classified as female. Unlike many emydid turtles, most Blanding's Turtle populations do not show significant size dimorphism between the sexes (Gibbons and Lovich, 1990). Males larger than the smallest gravid female we found (175 mm CL) were classified as adults, as we did not test for mature spermatozoa in males. Turtles below this size were considered juveniles. We examined the right pectoral scute for the presence of growth rings. Blanding's Turtles can be reliably aged to approximately 14 years (Congdon and van Loben Sels, 1991; Germano and Bury, 1998). Although it has been questioned whether growth rings are reliable in age-estimation (Brooks et al., 1997; Litzgus and Brooks, 1998a; Wilson et al., 2003), we included these estimates in order to gain a general idea of age at maturity. For the sake of brevity, we refer to age or years based on these rings; we acknowledge that these estimates hold only if rings are deposited annually. Using Mitutoyo dial or digital calipers, accurate to the hundredth of a millimeter, we measured the medial length of each ring to compare yearly growth (Germano et al., 2000) and recorded maximum carapace (CL) length to the nearest 0.1 mm. Turtles were released within 24 h at their original capture location unless gravid, in which case some were held for induced oviposition.

We estimated population size and survival probability using the six years of mark-recapture data and the Jolly-Seber method in program JOLLY (J. E. Hines, JOLLY Program for running capture-recapture models. United States Department of the Interior National Biological Service, Patuxent Environmental Science Center, Laurel, Maryland, 1990) with year as the sampling period. Likelihood ratio tests between models provided in the JOLLY output were used to determine the best-fitting model for the data (Langtimm et al., 1996). Model A is the general Jolly-Seber model that allows capture and survival probabilities to vary over sampling periods, and model B allows capture probabilities to vary, but not survival probabilities. In analyses where model B fit as well as model A, we used model A because it may be more accurate in predicting population size (n) than model B (Pollock et al., 1990). Due to low capture rates, juvenile parameters (population size and survivorship) were not estimated.

Reproductive traits.—We determined if females were gravid through palpation of the inguinal region or x-ray (2001–2003). Clutch size was determined by x-ray. We injected 79 gravid females with synthetic oxytocin to induce oviposition in a water-filled bucket. We measured eggs for length, width, and mass and incubated them at 28°C for use in other studies (Dinkelacker et al., 2004, 2005). We used least-squares linear regression analyses to determine relationships between maternal CL, clutch size, and egg measurements (length, width, and mass \pm 0.1 mm or 0.1 g). Pairwise correlations were used to examine relationships between egg measurements and clutch size, and partial correlations were used to control for body size. Following the method described by Congdon and Gibbons (1987), we measured pelvic aperture width (\pm 0.1 mm) using calipers at the narrowest point between the ilia on x-rays taken from 2001–2003 of 11 gravid turtles, as only 11 x-rays were clear enough to get accurate measurements. We then measured egg width (\pm 0.1 mm) on corresponding x-rays and examined the linear regressions of ilia width and egg width, using a one factor ANCOVA.

Statistical analyses.—We used non-parametric tests when the assumptions of the equivalent parametric test were not met (Zar, 1998). We conducted statistical tests in program JMP version 5.1 (SAS Institute, Cary, NC), with the exception of the one factor ANCOVA used to test the slopes between ilia width and egg width performed in the program Super-ANOVA (Abacus Concepts, Berkeley, CA). For all means, we report standard error. Only data from turtles caught in fyke nets were used for population/survivorship estimates, sex ratios, and adult:juvenile ratios in order to reduce bias in the results (i.e., turtles captured by hand on land were almost exclusively gravid females).

RESULTS

Demographics.—A total of 282 individual turtles were captured (including hand captures) during this study: 44 juveniles (15.6%), 84 males (29.7%), and 154 females (54.6%). The number of turtles captured in fyke nets was 223: 36 juveniles (16.1%), 79 males (35.4%), and 108 females (48.4%). The adult sex ratio was 0.7:1.0 M:F and was significantly different from 1:1 ($\chi^2 = 4.5$, $df = 1$, $P = 0.034$). The adult:juvenile ratio was 5:1. Adult male and

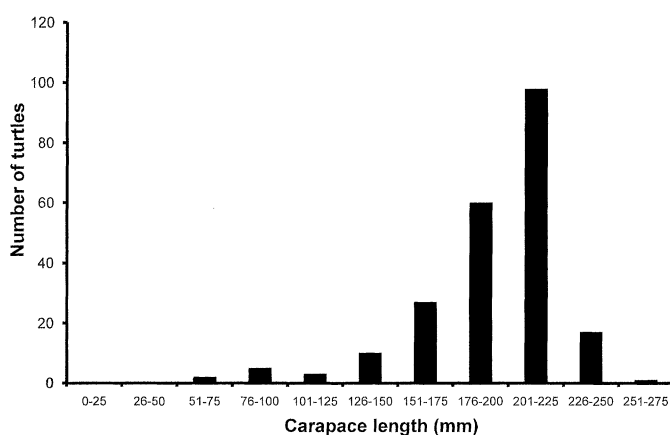
Table 1. Demographic and Reproductive Characteristics of Western Nebraska Blanding's Turtles. All means are shown ± 1 standard error; measurements are in mm and mass in g.

	<i>n</i>	Mean	Range
Adult male			
Carapace length	84	204.9 \pm 2.2	177.1–255.3
Adult female			
Carapace length	154	208.2 \pm 0.9	175.3–231.1
Clutch size	51	15.0 \pm 0.4	3.0–24.0
Egg*			
Mass	79	12.6 \pm 1.5	8.6–15.9
Length	79	36.1 \pm 1.7	31.3–39.4
Width	79	24.2 \pm 1.1	20.6–26.5

* For egg measurements, *n* = number of clutches; means are determined from clutch mean, not individual numbers of eggs (*n* = 1054).

female turtles were not dimorphic in CL (Wilcoxon test, $Z = 1.0$, $P = 0.317$; Table 1). The size distribution was skewed towards larger turtles (Fig. 1). Carapace length ranged from 64.0 mm (a juvenile) to 255.0 mm (a male). Examination of mean percent increase of the right pectoral scute rings indicated turtles grew fastest in their earlier years (Table 2). Adult population size was estimated to be 221 turtles (Table 3). Model A in JOLLY was found to be the best fit for population size and survivorship estimations. Female survivorship was lower than that of male turtles (Table 3).

Reproductive ecology.—We captured 170 gravid turtles from 2001–2006 (134 individuals). Eleven female turtles were gravid in two consecutive nesting seasons, and two females were gravid in three consecutive nesting seasons. Nesting seasons are defined as the first day a gravid female was found until the last day a gravid female was found. The percentage of females gravid when captured (fyke net captures only) during the nesting seasons of 2002–2006 ranged from 46% to 87% (mean = 72%). The smallest gravid female was 175 mm CL and older than 14 years. The largest gravid female was 231 mm CL and had more than 14 growth rings; the two youngest were both estimated to be 11 years (11 growth rings) and measured 187 mm and 207 mm CL, respectively.

**Fig. 1.** Size distribution of Blanding's Turtles (*Emydoidea blandingii*) from Beem Lake and Doc Lake, Grant County, Nebraska (*n* = 223). For turtles captured multiple times, the size at the most recent capture was used.**Table 2.** Size Increase in Right Pectoral Scute for western Nebraska Blanding's Turtles. The mean percentage increase (± 1 standard error) is shown for the right pectoral scute for each visible ring. Age was estimated from counting plastral rings.

Estimated age	<i>n</i>	Percentage increase
H	106	79.6 \pm 2.6
1	118	33.1 \pm 1.6
2	118	19.4 \pm 0.8
3	115	15.6 \pm 0.6
4	114	13.1 \pm 0.5
5	112	11.1 \pm 0.4
6	108	9.1 \pm 0.4
7	98	8.0 \pm 0.4
8	92	7.0 \pm 0.3
9	72	6.0 \pm 0.3
10	56	6.0 \pm 0.4
11	40	5.3 \pm 0.5
12	27	5.1 \pm 0.6
13	10	4.5 \pm 0.8

Seventy-nine individual gravid turtles were injected with oxytocin from 2001 to 2005. Linear regressions between mean maternal CL and mean egg measurements were significant, but no significant correlation was detected between maternal CL and clutch size (Table 4). A linear regression of data pooled from other studies indicates that across the range of Blanding's Turtles, clutch size increases with increasing CL (Fig. 2). Pairwise correlations found all egg measurements correlated with one another, but no correlation existed between clutch size and egg size (Table 4). To eliminate effects of maternal CL, partial correlations between clutch size and mean egg measurement (length, width, and mass) were used (*n* = 40 clutches), and were not significant (clutch size by egg length, $P = 0.995$; clutch size by egg width, $P = 0.268$; clutch size by egg mass, $P = 0.669$). Linear regression of mean egg width and pelvic width, varying with CL, showed that egg width increased at approximately the same rate as pelvic opening width (Fig. 3). A one factor ANCOVA with width as the dependent variable, CL as the independent variable, and ilia versus egg as the factor showed that the slopes were not significantly different from each other ($P = 0.909$).

DISCUSSION

Demographics.—The mean sizes and ranges of CL of adult Blanding's Turtles at the sites we studied were similar to those published by Rowe (1992) for western Nebraska.

Table 3. Mean Annual Survivorship and Population Size Estimates for Blanding's Turtles in Western Nebraska. An open population Jolly–Seber model was used for population estimations, *n* = the actual number of turtles captured. All means are shown ± 1 standard error.

	<i>n</i>	Survivorships (%)	Population size estimates
Adults	187	69.0 \pm 8.8	221 \pm 69
Adult male	79	90.0 \pm 20.6	111 \pm 44
Adult female	108	59.0 \pm 12.6	112 \pm 56

Table 4. Linear Regressions and Pairwise Correlations of Carapace Length, Clutch Size, and Egg Measurements. R^2 and r -values are reported. For carapace length with clutch size, $n = 51$ clutches; clutch size with egg measurements, $n = 40$ clutches; within egg measurement correlations, $n = 79$ clutches. All egg measurement results are based on the mean sizes per clutch, not individual eggs.

	Carapace length [†]	Egg width ^{††}	Egg length ^{††}	Egg mass ^{††}
Egg width	0.25*	—	—	—
Egg length	0.10*	0.56*	—	—
Egg mass	0.24*	0.91*	0.76*	—
Clutch size	0.02	0.19	0.18	0.13

* indicates significant R^2 (linear regression) or r -value (pairwise correlation) after Bonferroni adjustments ($P < 0.01$)
† indicates a linear regression
†† indicates a pairwise correlation

Considering that his study included the two sites we observed, this is not surprising. In nearby Valentine, Nebraska (approximately 180 km northeast), Germano et al. (2000) found adult male CL to average 203.7 mm, only 1 mm less than we found. However, mean CL for adult females found by Germano et al. (2000) was only 186.1 mm, much smaller than the mean size we found for adult females

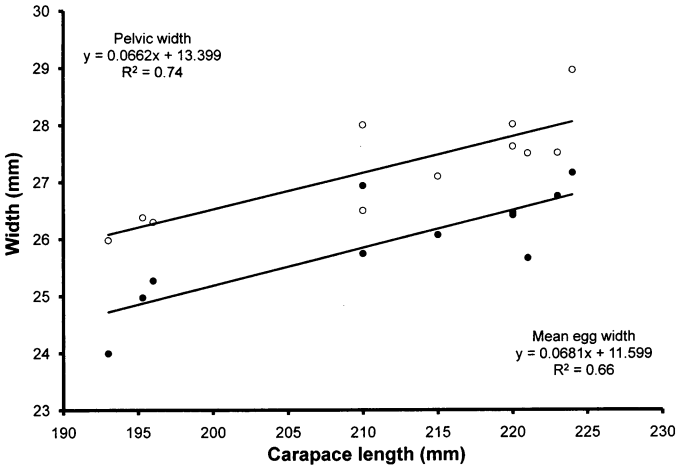


Fig. 3. Linear regressions between egg and pelvic aperture width and carapace length in Nebraska Blanding's Turtles, *Emydoidea blandingii* ($n = 11$). Egg width = filled circles and pelvic width = open circles.

(Table 1). This may be because Germano et al. (2000) used a smaller minimum size of 162 mm for adult females, while we used 175 mm for the smallest adult female. However, even if turtles presumed female (no sign of male characteristics) between 162 and 175 mm CL are added in from our population, the mean CL is 205.9 mm, still longer than that of Germano et al. (2000).

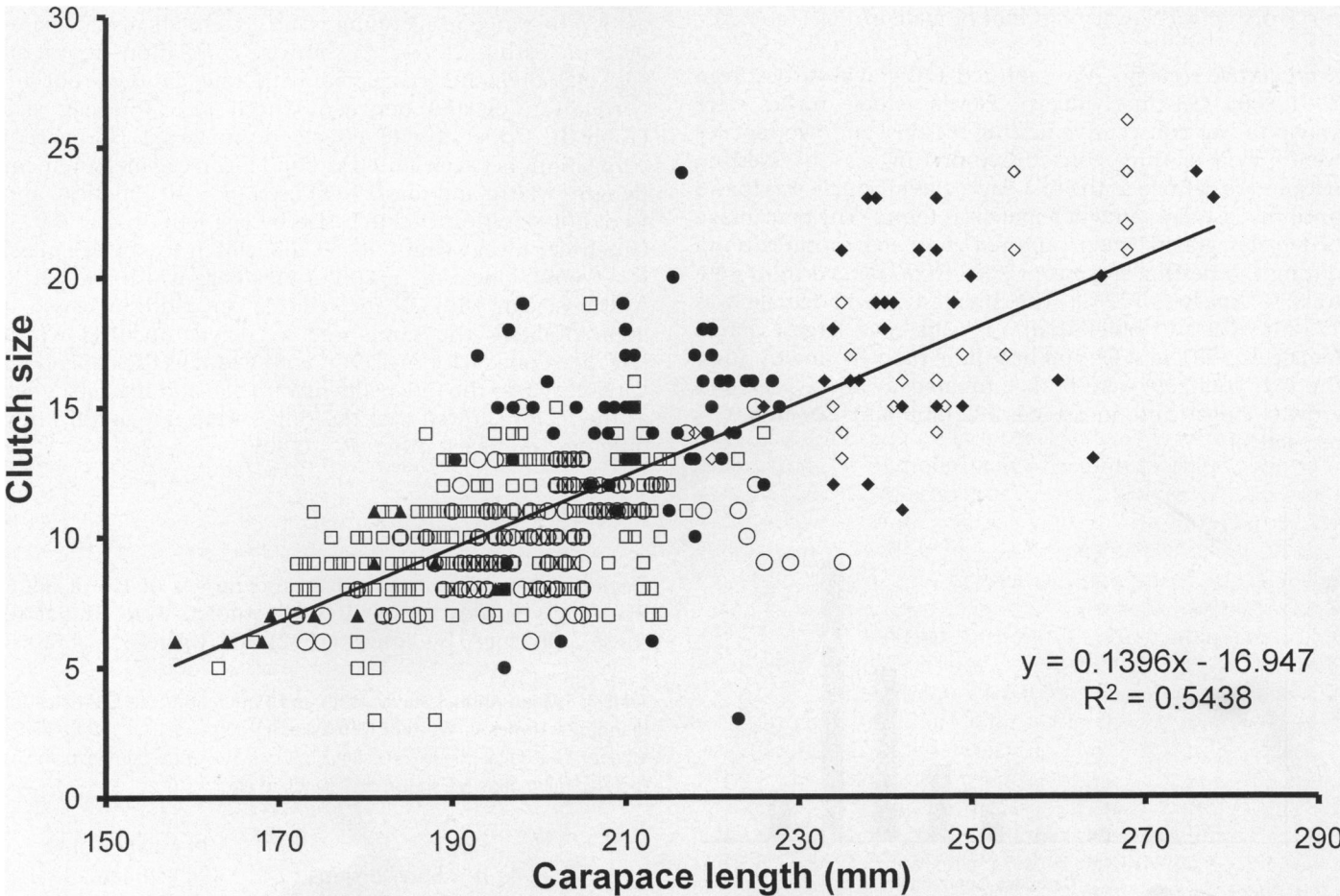


Fig. 2. Linear regression of clutch size and CL (carapace length) for Blanding's Turtles across their range. Nebraska ($n = 51$, this study) = filled circles; Ontario ($n = 11$, MacCulloch and Weller, 1988) = filled triangles; Michigan ($n = 170$, Congdon and van Loben Sels, 1991) = open squares; Camp Ripley, Minnesota ($n = 29$, Sajwaj et al., unpubl. data) = filled diamonds; Weaver Dunes, Minnesota ($n = 85$, Pappas et al., 2000) = open circles; Hennepin and Scott County, Minnesota ($n = 21$, M. Linck, unpubl. data) = open diamonds.

The mean body sizes of the western Nebraska population fall within those published across the species' range and the distribution is similar to those in other studies (McMaster and Herman, 2000; Pappas et al., 2000; Rubin et al., 2004). In fact, *post hoc* linear regressions indicate that in Blanding's Turtles, mean female body size (i.e., carapace length) does not follow a discernable pattern with latitude ($n = 3$; $P = 0.886$) or longitude ($n = 3$; $P = 0.808$). Adult females at approximately the same latitude range widely in mean CL from 176.5–208.2 mm (MacCulloch and Weller, 1988; Congdon and van Loben Sels, 1991; Germano et al., 2000). In regards to longitude, the mean CL reported for female Blanding's Turtles in Massachusetts (Graham and Doyle, 1979; 204 mm) and Maine (Joyal et al., 2000; 206 mm), both easterly populations, are similar to the mean size we report for females in this western Nebraska population (Table 1), implying there is no east–west size gradient. Previous studies of freshwater turtles have shown that turtle body size may increase with latitude (Iverson and Smith, 1993; Litzgus and Brooks, 1998b; Zuffi et al., 1999), although we found no evidence for this in Blanding's Turtles.

Several studies have found that male Blanding's Turtles have a significantly longer carapace than females (Graham and Doyle, 1979; Germano et al., 2000; Pappas et al., 2000). Although the longest turtles in our population were male (Table 1), we found no statistical evidence for dimorphism. In studies that did report sexual size dimorphism for Blanding's Turtles, the difference in mean size between male and female CL ranged from only 11.3–17.6 mm (Graham and Doyle, 1979; Germano et al., 2000; Pappas et al., 2000). We agree with Pappas et al. (2000) that it is questionable whether the reported sexual size dimorphism in Blanding's Turtles is biologically relevant, especially when compared to other freshwater turtle genera with true dimorphism (e.g., *Graptemys*, *Malaclemys*, *Pseudemys*; Ernst, 1994).

Growth (as percent increase) of Blanding's Turtles in our study was similar to that reported by other studies in that the fastest growth took place during the first few years, especially during years one and two (Graham and Doyle, 1977; Rowe, 1992; Germano et al., 2000; Table 2). Growth percent increase (79.6%) in the population we studied using annular widths of the right pectoral scute from hatching to year one was most similar to that reported by Graham and Doyle (1977; 81.4%) for a Massachusetts population. We found a higher growth rate for year one than did Rowe (1992; 70.1%). The difference may be because Rowe included three other populations in his analyses, we had a larger sample size, and we used pectoral rather than abdominal scutes. It is interesting to note that although the percent growth increase we found (Table 2) was lower than that in Valentine, Nebraska (Germano et al., 2000; 119.3% for year 1), the mean CL for adult turtles at our site was greater (mean 195.3 CL, Germano et al., 2000; mean 206.5 CL, this study). Congdon and van Loben Sels (1991, 1993) suggested that size variation of adult Blanding's Turtles within the same population is related to juvenile growth rates and differences in ages at maturity. Indeed, differences between the populations are probably related to variation in ages of maturity as well as juvenile growth rates.

Survival probabilities of adult Blanding's Turtles in this study (Table 3) were lower than those reported from Michigan by Congdon et al. (1993, 2000), who found an

adult survivorship probability of 0.96 during a 23-year study using mark–recapture techniques. The most likely explanation for this difference in survival probability is the presence of roads at our study sites. Roads may decrease survival rates, as turtles are particularly vulnerable to vehicular mortality (Ashley and Robinson, 1996). Female turtles in particular may encounter roads more frequently as they travel during nesting forays, hence lowering their survival probability (Steen and Gibbs, 2004; Aresco, 2005; Steen et al., 2006). The lowered survival of adult turtles could have serious consequences for the long-term survival of these western Nebraska populations, given that high adult survivorship is required to maintain stable populations in many species of turtles (Wilbur and Morin, 1988), including the Blanding's Turtle (Congdon et al., 1993). Alternately, there may simply be a trap bias towards males; because the survivorship estimate is based on recaptures, there is the possibility that females are not as likely to re-enter traps after initial captures. Considering that we do have a bias towards females in terms of sex ratio and that the actual population size estimate for females equals that of males, we cannot discount that our sampling technique may be flawed.

Demographic results were in concordance with other studies of Blanding's Turtles in regard to population composition. Female biased sex ratios have been noted in previous reports (Ross, 1989; Congdon and van Loben Sels, 1991; Pappas et al., 2000). *Emydoidea* exhibits temperature-dependent sex determination, with females produced at higher incubation temperatures (Gutzke and Packard, 1987). The tendency for Blanding's Turtle populations to be female biased may be the result of female turtles choosing the warmest possible nest sites available in the relatively cool northern temperate climates where this species occurs. Females in the western Nebraska population we studied frequently nested on railway embankments, especially south-facing slopes (pers. obs.), which because of sun exposure and less vegetative cover, may be warmer than surrounding areas. Although other factors, such as vegetative cover (Wilson, 1998) and distance from water (Spencer and Thompson, 2003) have been shown to influence turtle nest-site selection, this would not change the fact that many turtles are nesting along the railway embankments. Indeed, the lower amount of vegetation and proximity to the water at these nest sites may elevate ground temperatures as well (Wilson, 1998; Kolbe and Janzen, 2002), potentially skewing the sex ratio.

The high proportion of adults to juveniles we observed is reflected in the skew toward large turtles in the size distribution (Fig. 1). Studies of Blanding's Turtles have shown that juveniles use different microhabitats than adults, especially areas of shallower water and denser vegetation (Germano et al., 2000; Joyal et al., 2000; McMaster and Herman, 2000). Because we trapped mostly in deeper, more open water, we probably underrepresented juveniles in our samples. A lack of small juveniles has been observed in populations of other freshwater turtle species, probably due to differences in habitat use (Pluto and Bellis, 1986; Congdon et al., 1992). Alternatively, our population may experience unnaturally high predation rates upon nests and decreased juvenile recruitment.

We noted frequent predation on nests monitored for another study at this site (up to 90% in a given year, Ruane, unpubl. data). Raccoons were often seen dead on the road in the area and are a major predator of turtle nests (Congdon et

al., 2000; Mitro, 2003). Additionally, their abundance increases in human disturbed areas (Crooks and Soulé, 1999) such as near roadways. Predation rates also increase when turtles nest along the water's edge (Kolbe and Janzen, 2002; Spencer and Thompson, 2003; Marchand and Litvaitis, 2004), as many turtles in our study did, because they could not cross the train tracks. A prolonged decrease in juvenile survivorship could have dire consequences for Blanding's Turtle population persistence (Congdon et al., 2000). This would be especially true in roadside populations that may also experience increased adult mortality due to vehicles (Ashley and Robinson 1996; Gibbs and Shriver, 2002). We noted that all four species of turtles around our study lakes (*Chelydra serpentina*, *Chrysemys picta*, *Emydoidea blandingii*, and *Terrapene ornata*) commonly suffer vehicle-induced deaths. Due to their late maturity and long-life spans (>80 years, Congdon et al., 2001), detecting changes in sex ratio and juvenile survival of turtles requires extensive long-term studies.

Reproductive traits.—Although the reproductive traits of this western Nebraska population were in some ways similar to those reported elsewhere, the differences we found exemplify why detailed examinations of individual populations are important. While it is accepted that Blanding's Turtles produce a maximum of one clutch per year (Ernst et al., 1994), it has been posited that they do not nest annually (Congdon et al., 1983; Pappas et al., 2000). The data we collected also indicate that Blanding's Turtles do not nest more than once per annum. However, the two turtles we found nesting in three consecutive years, the 11 turtles we found nesting in two consecutive years, and the high minimum percentage (72%) of gravid females suggests that annual nesting may be typical in our population. Due to the large size of the study areas, it was impossible to determine whether each adult female turtle reproduced every year. Females captured gravid one year and then captured non-gravid the following year were frequently captured after their previously known nesting date. Hence, nesting may have occurred before we re-captured a particular female.

Female turtles in western Nebraska appear to mature near 175 mm CL (minimum size of gravid female captured). The smallest gravid female found by Rowe (1992) was 203 mm CL, considerably larger than the smallest gravid female we found, and was probably due to his smaller sample size. At Valentine, Nebraska, Germano et al. (2000) estimated the smallest mature female at 162 mm CL, based on secondary sexual characteristics. Because we used the smallest gravid female found to determine size at maturity, our estimate may be conservative, and females in our population may be maturing at smaller sizes. Other populations certainly mature at smaller CL (Fig. 2). Germano et al. (2000) estimated age of maturity in Valentine, Nebraska to be ten years for females. While our data support this, with the two youngest gravid females both estimated to be 11 years old, there was a large discrepancy in body sizes between these two females (187 and 206 mm CL). Germano et al. (2000) estimated that turtles ten years old at his site would be 173 mm CL. Considering the difference in sizes at age 11 and the estimation of CL at age 10 by Germano et al. (2000), the validity of growth models to predict maturity across different locales is questionable, even across short distances. Blanding's Turtles mature at various sizes and ages across their range (Adams and Clark, 1958; Graham and Doyle,

1979; Sajwaj et al., unpubl. data), and growth models may not be appropriate for this species as a whole.

Mean egg length and mean egg mass at the western Nebraska site were all similar to those reported in other studies (Congdon and van Loben Sels, 1991; Rowe, 1992; Pappas et al., 2000); however, mean egg width was greater than those in previously published reports (Congdon and van Loben Sels, 1991; Rowe, 1992; Pappas et al., 2000; Table 3). Interestingly, the mean clutch size we found was also larger than reported in most studies (Congdon and van Loben Sels, 1991; Rowe, 1992; Pappas et al., 2000), but had no correlation with maternal CL, contrary to previous studies (MacCulloch and Weller, 1988; Congdon and van Loben Sels, 1991; Pappas et al., 2000). The significant correlations between maternal CL and all egg dimensions that we found (Table 4) have not been previously reported in Blanding's Turtles (MacCulloch and Weller, 1988; Congdon and van Loben Sels, 1991; Rowe, 1992). Unlike females in populations that increase clutch size with body size, females in this western Nebraska population may optimize hatchling size (and hence fitness) by producing larger eggs. Blanding's Turtles belong to the subfamily Emydinae, which contains the genera *Actinemys*, *Clemmys*, *Emydoidea*, *Emys*, *Terrapene*, and *Glyptemys* (Stephens and Wiens, 2003). The reproductive strategy in this clade appears to be the increase in clutch size with increases in body size, rather than increases in egg size (Litzgus and Brooks, 1998b; Zuffi et al., 1999; Lovich and Meyer, 2002; but see Brooks et al., 1992). This is generally true for Blanding's Turtles across most populations (Fig. 2), even though the population in this study does not conform.

A potential explanation for an increase in egg size rather than clutch size in the western Nebraska population is based on the arid conditions of the Nebraska Sandhills. Unlike regions occupied by other semi-aquatic emydine turtles (with exception of Mojave Desert populations of *Actinemys marmorata*), annual precipitation is quite low at 45.6 cm in Grant County, Nebraska (World Climate Data, <http://www.worldclimate.com/>, 2007). Previous studies have demonstrated that larger turtles are more resistant to desiccation than smaller turtles (Bodie and Semlitsch, 2000; Costanzo et al., 2001; Finkler, 2001). Because Blanding's Turtle hatchlings may actually overwinter on land (Dinkelacker et al., 2004), there is a risk of desiccation during hibernation. In a dry region, producing the largest hatchlings possible may be more adaptive than producing many small hatchlings. Within populations of the Desert Tortoise (*Gopherus agassizii*), those living in erratic climates produce larger eggs than tortoises in areas where rainfall is more predictable (Wallis et al., 1999). If Blanding's Turtles in the Sandhills are countering the xeric habitat by producing the largest eggs possible, one might expect a similar response from a closely related species, such as *A. marmorata* in the Mojave Desert, but this is not the case (Lovich and Meyer, 2002). However, when compared to Blanding's Turtles in western Nebraska, *A. marmorata* hatchlings have a shorter hibernation period that may limit desiccation and also reside in a habitat where flooding of the nest may occur, reducing desiccation (Lovich and Meyer, 2002).

Optimal egg size theory states that natural selection should optimize egg size to a point where an increase in egg size no longer holds reproductive benefits; instead, increases in clutch size are more advantageous (Smith and Fretwell, 1974; Brockelman, 1975). However, some species

of turtles may not conform to optimal egg size theory because of pelvic canal constraints on maximum egg size (Congdon and Gibbons, 1987; Clark et al., 2001; Bowden et al., 2004), although this is not necessarily expected in a large-bodied species such as the Blanding's Turtle (see Congdon and Gibbons, 1987 regarding *Trachemys scripta*). However, the increase of egg width with CL in our western Nebraska population supports that optimal egg size has not been reached (Fig. 3). Furthermore, the ANCOVA results support that egg width and ilia width are increasing at the same rate. Congdon and Gibbons (1987) found similar results in *Deirochelys reticularia* and *Chrysemys picta* and concluded that the size of the pelvic aperture was constraining eggs from reaching optimal (larger) size. The lack of an inverse correlation between egg size and clutch size lends support to the notion that female Blanding's Turtles in the western Nebraska population are allocating accumulated energy to egg size, not clutch size, and it may be due to the superior desiccation resistance offered to larger eggs/hatchlings. This trend occurs in several species of turtle and supports the view that many species of turtle do not, or cannot, conform to optimal egg size theory (Congdon and Gibbons, 1985; Bernardo, 1996; Wilkinson and Gibbons, 2005). To further clarify this relationship, a larger sampling of gravid female Blanding's Turtles' x-rays is required.

Our study of western Nebraska Blanding's Turtles illustrates the need for the examination of conspecific populations across a species' geographic range. Reproductive traits are vital data when management plans are formed, and, as our study implies, they need to be determined for individual populations. Additionally, an understanding of how variation in habitat and local environmental conditions (i.e., aridity) affect reproduction are necessary to best evaluate conservation plans for the future, especially given threats such as global climate change. Although populations of western Nebraska Blanding's Turtle are in many ways similar to their counterparts in other regions, their unique relationship between egg size and body size suggests that variation can be substantial. Combined with evidence from other species that vary in some reproductive trait (Iverson and Smith, 1993; Wallis et al., 1999; Litzgus and Mousseau, 2003), our data suggest that detailed studies should be undertaken for turtle species living across a large geographic range and in diverse habitats.

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